ISSN (print) 0093-4666 © 2015. Mycotaxon, Ltd. ISSN (online) 2154-8889

MYCOTAXON

http://dx.doi.org/10.5248/130.207

Volume 130, pp. 207–213 *January–March 2015*

Distribution of *Alternaria* species among sections. 1. Section *Porri*

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Abstract — The evaluation of all available descriptions of *Alternaria* species allowed the assignment of another 71 species to *A.* sect. *Porri*, in addition to the 46 species previously included on the basis of phylogenetic analysis. We assess that this section encompasses 117 species, which are listed. An emended and somewhat expanded description of *A.* sect. *Porri* is presented.

Key words — *Nimbya*, *N. rhapontici*

Introduction

The genus *Alternaria* Nees is a large taxonomic group that comprises approximately 280 species (Simmons 2007). A series of large-scale works has attempted to resolve the phylogeny of *Alternaria* and other alternarioid hyphomycetes by employing more than ten different genomic loci (Pryor & Bigelow 2003; Hong et al. 2005; Runa et al. 2009; Lawrence et al. 2012, 2013, 2014; Woudenberg et al. 2013). Several well-supported phylogenetic lineages have been revealed within the alternarioid hyphomycetes that have led to several taxonomic novelties. The genus *Alternaria* was divided into eight taxonomic sections by Lawrence et al. (2013). According to an alternative concept (Woudenberg et al. 2013) all alternarioid hyphomycetes were collapsed into one genus, *Alternaria*, with 24 sections, 11 of which referred to *Alternaria* sensu stricto.

The monophyletic status of the so-called large-spored species was supported by all analyses. Both research groups (Lawrence et al. 2013; Woudenberg et al. 2013) agreed that the group of large-spored species should be treated as a well-defined section of the genus, *Alternaria* sect. *Porri*, based on phylogenetic as well as morphological data. Forty-six species were included in the section

by Lawrence et al. (2013). However, the size of the section was estimated to comprise c. 120 (Gannibal 2012) or c. 80 (Woudenberg et al. 2013) species. *Alternaria porri* was chosen as type species. Only one large-spored species, *A. helianthiinficiens* E.G. Simmons et al., was placed apart from section *Porri* (Woudenberg et al. 2013).

The main discriminating morphological features of many *Alternaria* sect. *Porri* species are larger conidia and the presence of a long filiform apical beak (Lawrence et al. 2013, Woudenberg et al. 2013). Sexual morphs have not yet been discovered. Probably all species in this section are parasites of plants. Species of *A.* sect. *Porri* have a rather strong substrate specialization and usually infect either a single plant species or only few species within a single family.

It is unlikely that all 280 *Alternaria* species will be molecularly characterized in the foreseeable future. Moreover, for several species, living isolates are not known and herbarium material is mostly too old and scanty for successful DNA extractions. On the other hand, the morphological diversity of *Alternaria* is well studied and available in a monograph published by Simmons (2007). Classical comparative morphology can be utilized to establish the affiliation of all *Alternaria* species to a specific section.

The aim of this work was to detect among phylogenetically unexamined *Alternaria* species, as far as possible, all species that fit the current morphological circumscription of *A.* sect. *Porri* and to emend the morphological concept of this section to reflect its extended membership.

Materials & methods

Morphology of almost all *Alternaria* species with legitimate names was analyzed with regard to conformity with criteria of *Alternaria* sect. *Porri*. The morphological assessment was based predominantly on descriptions made by Simmons (2007). Species described after 2007 were assessed using original diagnoses and illustrations. Descriptions of eight species included in *A.* sect. *Porri* were found in Sun & Zhang 2007 (*A. lactucicola* and *A. rhaponticicola*); Labuda et al. 2008 (*A. jesenskae*); Zhang & Zhang 2008 (*A. amphicarpaeae*, *A. sojae*, and *A. tribuli*); and Gannibal 2010 (*A. simmonsii* and *A. silybi*). Two conceptions of *A.* sect. *Porri* were used for comparison, those of Lawrence et al. (2013) and Woudenberg et al. (2013).

Results & discussion

The evaluation of all available descriptions of *Alternaria* species allowed for the addition of 71 species to *A.* sect. *Porri*. The size of this section is assessed to comprise 117 species. *Alternaria* species of *A.* sect. *Porri* are listed in Table 1.

Eight species for which living specimens are not available—*A. bannaensis* W.Q. Chen & T.Y. Zhang, *A. basellae* T.Y. Zhang, *A. calystegiae* Nelen, *A. ellisii* Pandotra & Ganguly, *A. iridicola* (Ellis & Everh.) J.A. Elliott, *A. nicotiana* J.L. Cheng, *A. nyctanthis* K.B. Deshp. & Rajd., and *A. trachelospermicola* (T.Y. Zhang

Table 1. List of *Alternaria* spp. assigned to *A.* sect. *Porri*.

***A. acalyphae* (Nelen) E.G. Simmons [a]**
***A. acalyphicola* E.G. Simmons** (Lawrence et al. 2013)
A. africana E.G. Simmons [b]
***A. agerati* Sawada ex E.G. Simmons** (Lawrence et al. 2013)
***A. agripestis* E.G. Simmons & K. Mort.** (Lawrence et al. 2013)
A. allii Nolla
A. amphicarpaeae Meng Zhang & T.Y. Zhang
***A. anagallidis* A. Raabe** (Lawrence et al. 2013)
A. anodae E.G. Simmons
***A. aragakii* E.G. Simmons** (Lawrence et al. 2013)
***A. argyroxiphii* E.G. Simmons & Aragaki** (Lawrence et al. 2013)
A. ascaloniae E.G. Simmons & C.F. Hill
A. azadirachtae E.G. Simmons & Alcorn
***A. bataticola* Ikata ex W. Yamam.** (de Hoog & Horre 2002; Lawrence et al. 2013)
A. beringelae E.G. Simmons
A. beticola E.G. Simmons & C.F. Hill
***A. blumeae* E.G. Simmons & Sontirat** (Hong et al. 2005; Lawrence et al. 2013)
A. bonducellae R. Dubey et al. [b]
A. brasiliensis F.M. Queiroz et al.
***A. calendulae* Ondřej** (Lawrence et al. 2013)
***A. capsici* E.G. Simmons** (Hong et al. 2005; Lawrence et al. 2013)
A. caricae T.Y. Zhang et al. [b]
***A. carthami* S. Chowdhury** (Lawrence et al. 2013)
***A. cassiae* Jurair & A. Khan** (Lawrence et al. 2013)
A. catharanthi (T.Y. Zhang & X.F. Lin) E.G. Simmons [b]
A. centaureae E.G. Simmons
A. cepulicola V.G. Rao [b]
A. ciceris E.G. Simmons
***A. cichorii* Nattrass** (Lawrence et al. 2013)
***A. cirsinoxia* E.G. Simmons & K. Mort.** (Lawrence et al. 2013)
***A. crassa* (Sacc.) Rands** (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013)
***A. cretica* E.G. Simmons & Vakal.** (Lawrence et al. 2013)
A. cucumericola E.G. Simmons & C.F. Hill
***A. cucumerina* (Ellis & Everh.) J.A. Elliott** (Hong et al. 2005; Lawrence et al. 2013)
A. cyamopsidis Rangaswami & A.V. Rao
***A. cyphomandrae* E.G. Simmons** (Lawrence et al. 2013)
***A. danida* E.G. Simmons** (Lawrence et al. 2013)
A. daturicola T.Y. Zhang et al. [b]
***A. dauci* (J.G. Kühn) J.W. Groves & Skolko** (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
***A. dichondrae* Gambogi et al.** (Lawrence et al. 2013)
A. echinaceae E.G. Simmons & C.F. Hill
A. eichhorniae Nag Raj & Ponnappa
A. enydrae S.A. Khan & M. Kamal [b]
A. euphorbiae (Barthol.) Aragaki & J.Y. Uchida [b]
***A. euphorbiicola* E.G. Simmons & Engelhard** (Hong et al. 2005; Lawrence et al. 2013)
A. flagelloidea (G.F. Atk.) Luttr. [b]
A. gaurae E.G. Simmons & C.F. Hill

A. glyceriae E.G. Simmons & C.F. Hill
***A. grandis* E.G. Simmons** (Lawrence et al. 2013)
A. guangxiensis W.Q. Chen & T.Y. Zhang [b]
***A. hawaiiensis* E.G. Simmons** (Lawrence et al. 2013)
A. heliophytonis E.G. Simmons
A. herbiculinae E.G. Simmons
A. hibiscinficiens E.G. Simmons & C.F. Hill
A. hordeiseminis E.G. Simmons & G.F. Laundon
A. hortensiae Unamuno ex E.G. Simmons [b]
A. iranica E.G. Simmons & Ghosta
A. jesenskae Labuda et al.
A. lactucicola X. Sun & T.Y. Zhang
A. lallemantiae (Khokhr.) E.G. Simmons [c]
A. latispora T.Y. Zhang & Meng Zhang [b]
***A. limicola* E.G. Simmons & M.E. Palm** (Lawrence et al. 2013)
A. linariae (Neerg.) E.G. Simmons
***A. linicola* J.W. Groves & Skolko** (de Hoog & Horre 2002; Lawrence et al. 2013)
A. longirostrata T.Y. Zhang & Meng Zhang [b]
A. loofahae E.G. Simmons & Aragaki
A. lunariae (Oudem. & C.J.J. Hall) E.G. Simmons [b]
***A. macrospora* Zimm.** (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
A. montanica E.G. Simmons & Robeson
***A. multirostrata* E.G. Simmons & C.R. Jacks.** (Lawrence et al. 2013)
A. nattrassii E.G. Simmons [b]
***A. nitrimali* E.G. Simmons & M.E. Palm** (Lawrence et al. 2013)
A. novae-guineensis E.G. Simmons & C.F. Hill
A. obtecta E.G. Simmons
***A. passiflorae* J.H. Simmonds** (Lawrence et al. 2013)
A. petasitis M. Kubota et al. [b]
A. pipionipisi E.G. Simmons
***A. poonensis* Ragunath** (Lawrence et al. 2013)
***A. porri* (Ellis) Cif.** (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
***A. protenta* E.G. Simmons** (Lawrence et al. 2013)
***A. pseudorostrata* E.G. Simmons** (Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
A. pulcherrimae T.Y. Zhang & J.C. David
A. ranunculi E.G. Simmons
A. readeri (G. Winter) Neerg. [b]
A. rhaponticicola X. Sun & T.Y. Zhang
***A. ricini* (Yoshii) Hansf.** (Lawrence et al. 2013)
A. rosa-sinensis M.X. Gao & T.Y. Zhang [b]
A. rosifolii E.G. Simmons & C.F. Hill
***A. rostellata* E.G. Simmons** (Lawrence et al. 2013)
A. saposhnikoviae J.Z. Zhang & T.Y. Zhang [b]
A. sauropodis E.G. Simmons
***A. scorzonerae* (Aderh.) Loer.** (Lawrence et al. 2013)
***A. sesami* (E. Kawam.) Mohanty & Behera** (de Hoog & Horre 2002; Lawrence et al. 2013)

A. sidae E.G. Simmons
A. silybi Gannibal
A. simmonsii Gannibal
A. sojae Meng Zhang & T.Y. Zhang
***A. solani* Sorauer** (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
A. solani-nigri R. Dubey et al. (Lawrence et al. 2013)
A. spinaciae Allesch. & F. Noack [b]
A. stachytarpheticola E.G. Simmons [b]
***A. steviae* Ishiba et al.** (Lawrence et al. 2013)
***A. subcylindrica* E.G. Simmons & R.G. Roberts** (Lawrence et al. 2013)
A. subtropica E.G. Simmons [b]
A. sudanensis E.G. Simmons [b]
A. tabasco E.G. Simmons & R.G. Roberts
***A. tagetica* S.K. Shome & Mustafee** (Lawrence et al. 2013; Woudenberg et al. 2013)
A. thunbergiae E.G. Simmons & Alcorn
A. tillandsiae E.G. Simmons & C.F. Hill
A. tomato (Cooke) L.R. Jones [d]
***A. tomatophila* E.G. Simmons** (Lawrence et al. 2013)
A. tribuli Meng Zhang & T.Y. Zhang
***A. tropica* E.G. Simmons** (Lawrence et al. 2013)
A. vanuatuensis E.G. Simmons & C.F. Hill
A. venezuelensis E.G. Simmons & Rumbos
A. viciae-fabae E.G. Simmons & G.F. Laundon
A. zinniae M.B. Ellis (Lawrence et al. 2013)

Bold font names = species with phylogenetic data (in the cited references).
Unannotated names = species with reliable living cultures and herbarium specimens.
Names with square bracketed annotations = species with herbarium specimens as the only available reliable material:
[a] = representative isolates have not been chosen;.
[b] = no known living isolates;
[c] = isolates are non-sporulating;
[d] = isolates are not correctly identified.

et al.) E.G. Simmons—were found to have intermediate characteristics that do not allow unambiguous placement in *A.* sect. *Porri* or any other section. Dubious morphological traits and the absence of isolates for detailed morphological or molecular studies make it impossible to assess their phylogenetic positions within the genus.

An isolate of *A. tomato* (CBS 114.35, deposited in 1935) clustered with strong support in the autonymous clade, *Alternaria* sect. *Alternaria* (Lawrence et al. 2013). However, the credible species description in Simmons (2007) suggests that this species resides in *A.* sect. *Porri*. According to Simmons (2007), no correctly identified *A. tomato* isolates are known. Hence, we suggest that *A. tomato* sensu Simmons belongs in *A.* sect. *Porri*.

Phylogenetic data revealed the polyphyletic nature of the genus *Nimbya* E.G. Simmons (Lawrence et al. 2012). Only four studied species from *Cyperaceae*

and *Juncaceae* clustered together as a separate clade ("true" *Nimbya*) when three species from *Amaranthaceae* were placed in *Alternaria* sect. *Alternantherae* (Lawrence et al. 2012, 2013). There are five *Nimbya* species found on plants other than *Cyperaceae*, *Juncaceae*, and *Amaranthaceae*, which likely belong to other clades. They have relatively large conidia and some of them could be related to the group of large-spored *Alternaria* species. At least *N. rhapontici* (Nelen) E.G. Simmons is morphologically very similar to *Alternaria* sect. *Porri,* but additional examinations are necessary to clarify the phylogeny and taxonomy of this species.

Here we present an emended and somewhat expanded description of the section:

Alternaria* sect. *Porri D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013; emend. Gannibal.

On V-8 primary conidiophores short, moderately long (up to 150–250 µm) or rarely very long (up to 700 µm or probably even longer [*A. pseudorostrata*, *A. nitrimali*]), simple or branched, with one or few (up to 9 on branched conidiophore [*A. solani*]) conidiogenous loci. Conidia solitary, in short or rarely moderately long chains (up to 7 units on PCA [*A. pseudorostrata*, *A. euphorbiicola*]), simple or with solitary lateral conidia, body of mature conidia moderately large (40–110 × 11–25(–30) µm), broadly ovoid, obclavate, ellipsoid, subcylindrical, or obovoid, disto- and euseptate, slightly constricted at septa, number of transepta in the conidial body varying from 7–9 [*A. cirsinoxia*] to 12–19 [*A. crassa*, *A. grandis*], with a single septum or 2–3 longitudinal septa in one or almost all transverse divisions; conidia of some species almost always without any longitudinal septa [*A. agripestis*, *A. subcylindrica*], pale yellowish tan to dark olivaceous brown, smooth or punctulate, at least some mature conidia with terminal beaks, solitary or in groups (up to 5) appearing as several beaks or a single beak with several branches, beaks aseptate or septate, 50–300(–460) µm long and (4–)5–6(–8) µm wide near the base, apex tapering to 1.5–3 µm or giving rise in secondary conidiophores. Conidia may form lateral or apical secondary conidiophores without filiform portion, sometimes with one or only few lateral secondary conidiophores arising from the body or beak.

In comparison with V-8, on PCA conidia are somewhat larger and have beaks with larger average numbers of branches (Simmons 2007; Gannibal et al. 2014).

Acknowledgments

It is my pleasure to acknowledge the attention of Dr. Uwe Braun and Dr. Daniel Lawrence for their presubmission reviews of this article. This work was supported by Russian Science Foundation (project #14-26-00067).

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